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Nutrient resorption and its influencing factors of typical desert plants in different habitats on the northern margin of the Tarim Basin, China

ZHOU Chongpeng[1,2], GONG Lu[1,2*], WU Xue[1,2], LUO Yan[1,2]

[1] College of Ecology and Environment, Xinjiang University, Urumqi 830017, China;
[2] Key Laboratory of Oasis Ecology, Ministry of Education, Urumqi 830017, China

Abstract: The resorption of nutrients from senescent leaves allows plants to conserve and recycle nutrients. To explore the adaptation strategies of desert plants to nutrient-limited environments, we selected four typical desert plants (*Populus euphratica* Oliv., *Tamarix ramosissima* Ledeb., *Glycyrrhiza inflata* Batal., and *Alhagi camelorum* Fisch.) growing in the desert area of the northern margin of the Tarim Basin, China. The contents of nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and Ferrum (Fe) in the leaves of these four typical desert plants and their resorption characteristics were analyzed. The relationship of nutrient resorption efficiency with leaf functional traits and soil physical-chemical properties in two different habitats (saline-alkali land and sandy land) was discussed. The results showed that the four plants resorbed most of the elements. Ca was enriched in the leaves of *P. euphratica*, *G. inflate*, and *A. camelorum*; Mg was enriched in the leaves of *G. inflata*; and Fe was enriched in the leaves of the four plants. The results of the redundancy analysis showed that leaf thickness, soil electrical conductivity, and soil P content were the major factors affecting the nutrient resorption efficiency of the four plants. Leaf thickness was negatively correlated with N resorption efficiency (NRE), P resorption efficiency, and Fe resorption efficiency; soil electrical conductivity was positively correlated with the resorption efficiency of most elements; and soil P content was negatively correlated with the resorption efficiency of most elements in the plant leaves. The results showed that soil physical-chemical properties and soil nutrient contents had an important impact on the nutrient resorption of plant leaves. The same species growing in different habitats also differed in their resorption of different elements. The soil environment of plants and the biological characteristics of plant leaves affected the resorption of nutrient elements in different plants. The purpose of this study is to provide small-scale data support for the protection of ecosystems in nutrient-deficient areas by studying leaf functional strategies and nutrient conservation mechanisms of several typical desert plants.

Keywords: nutrient resorption; leaf functional traits; soil physical-chemical properties; resorption efficiency; different habitats; desert plants

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1 Introduction

Nutrient resorption refers to the process by which perennial plants retranslocate nutrients before senescent tissues fall off and store them in other living tissues (Han et al., 2013). Desert plants

*Corresponding author: GONG Lu (E-mail: gonglu721@163.com)
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have evolved a variety of unique nutrient utilization strategies under long-term environmental conditions, such as water and salt stress, high temperature and drought stress, and nutrient limitation. For example, some desert shrubs generally put most of their biomass into underground organs (well-developed root systems) to obtain more water and nutrients, and some desert plants protect seeds from stressful environments, such as nutrient deficiency, by delaying seed dispersal (Abdi et al., 2019; Teresa et al., 2021). The nutrient resorption strategy is also an important nutrient utilization strategy. Nutrient resorption strategies increase plant nutrient use efficiency while reducing the dependence of plants on soil nutrient supply during growth (Aerts, 1996). Research on the nutrient resorption of desert plants is helpful for further exploring the resource utilization strategy of plants and has important scientific significance for further revealing the adaptation mechanism of desert plants to adverse conditions.

The nutrient resorption efficiency of plants is affected by biotic and abiotic factors, so it is not only affected by the biological characteristics of plants, but also by environmental factors (Aerts et al., 2000). Studies on the response of plant nutrient resorption to the environment have mostly focused on natural environmental factors such as latitude, temperature, rainfall pattern, and exogenous fertilization (Li et al., 2014; Sardans et al., 2017; Prieto et al., 2020; Liu et al., 2021), and most of the research on nutrient resorption has focused on non-desert plants (Zeng et al., 2005; Wei et al., 2020; Zhu et al., 2022). Element research has mostly focused on the study of restrictive elements such as nitrogen (N) and phosphorus (P) (Zhang et al., 2015; Rea et al., 2018), but less attention has been given to other elements. Studies on desert plants have found that N resorption efficiency (NRE) and P resorption efficiency (PRE) of some halophytes in arid areas increase significantly with increasing water stress, drought index, and salt stress (Luo et al., 2021). Studies have also shown that soil nutrients and plant nutrient resorption are negatively correlated at large scales, but in small-scale regions, the nutrient resorption of some plants is not significantly correlated or positively correlated with soil nutrients (Zhang et al., 2015). In environments with limited nutrients, plants often have higher nutrient resorption efficiency. The limited nutrient conditions in the desert environment make perennial desert plants more dependent on nutrient resorption mechanisms than non-desert plants (Zhang, 2018). Some studies have also found that desert plants will have early leaf litter due to drought and other factors, and the drier the habitat, the lower the nutrient resorption rate of the species (Li et al., 2021). To better understand the nutrient reutilization of desert plants and their response to environmental changes, it is urgent to explore the different nutrient strategies derived from perennial desert plants and their influencing factors.

The desert area on the northern margin of the Tarim Basin is located in the upper reaches of the Tarim River and the northern part of the Taklimakan Desert. It is one of the key areas for biodiversity conservation and global change research in China (An et al., 2017). The region is extremely arid with harsh conditions, scarce precipitation, and intense evaporation. Desert plants have formed their own adaptation strategies through long-term evolution (Luo et al., 2017; Liu et al., 2021; Wei et al., 2021), but the mechanism of nutrient resorption is not clear. Therefore, four typical desert plants in this area were selected in this study. They are widely distributed in deserts and have important ecological value for serving as windbreaks, fixing sand, and maintaining ecosystem balance. They appear simultaneously in two different habitats. By analyzing their nutrient resorption characteristics, combined with leaf functional traits and soil physical-chemical properties, we discussed the influencing factors of nutrient resorption in desert plant leaves in this study. The purpose of this study was to provide a scientific reference for studying the element cycling mechanism of vegetation and soil in arid areas and to lay a theoretical basis for the protection and restoration of desert ecosystems. We hypothesized that the higher the degree of salinization, the higher the resorption efficiency of plant leaves on various nutrients, and soil physical-chemical properties and leaf functional traits of plants will jointly affect plant nutrient resorption.

2 Materials and methods

2.1 Study area

The study area (40°41′–40°42′N, 80°58′–81°15′E) is located in the northern margin of the Tarim Basin in Xinjiang Uygur Autonomous Region of China. The terrain slopes from northwest to south. The northern part is the agricultural area of the Tarim River alluvial plain, and the eastern and southern parts are the Taklimakan Desert, which has a warm temperate continental arid climate. The annual mean temperature is approximately 10°C, and the mean annual precipitation is less than 50 mm, with strong evaporation, large temperature differences, numerous sunshine hours, and rich light and heat resources. The area belongs to a typical desert ecosystem, and the soil formation is relatively simple. The soil types are mainly sandy soil and saline soil. The soil parent material is mainly brown desert soil. The vegetation types in the study area are mainly shrubs and herbs. The dominant plant species are *Populus euphratica* Oliv., *Tamarix ramosissima* Ledeb., *Glycyrrhiza inflata* Batal., *Alhagi camelorum* Fisch., *Nitraria tangutorum* Bobr., and *Kalidium foliatum* (Pall.) Moq..

2.2 Experimental design and samples collection

In this study, four dominant plants, *P. euphratica*, *T. ramosissima*, *G. inflate*, and *A. camelorum*, growing in the desert area of the northern margin of the Tarim Basin were selected as research objects. In the desert area of the northern margin of the Tarim Basin, we selected two different habitats, including saline-alkali land (Habitat I) and sandy land (Habitat II), according to their distances from the oasis. The soil of Habitat I is mainly aeolian sandy soil, and this habitat is distributed on the edge of the Taklimakan Desert. The soil type of Habitat II is saline soil, and this habitat is distributed in the ecotone between farmland and wasteland and next to abandoned farmland. The soil of both habitats is alkaline, the soil water content is low, and all four plants grow at the same time. We selected three plots with an area of 20 m×20 m in each habitat. The selection of plots was based on the principle of representativeness. Given the site environments have generally the same topographic factors such as altitude and aspect, we selected the areas with less human disturbance. In June 2021, mature leaves were collected from randomly selected plants in the plot, and several plants of similar size and growth were selected for each plant (5 plants for *P. euphratica* and *T. ramosissima* and 10 plants for *G. inflata* and *A. camelorum*). The selected plants were marked with red cloth strips, and senescent leaves were collected from previously marked species in October 2021. For each selected plant, fully extended, complete, and sufficient leaves were collected (the number of collected leaves depended on the shape and size of the plant leaves). Half of the collected leaves were stored in a numbered sample bag for subsequent element content determination, and the other half were stored in a dark environment and kept fresh at low temperature for morphological analysis and chlorophyll content determination. Each sample was replicated not less than five times. At the same time, soil samples (0–20 cm below the plant canopy) were collected in each quadrat (after removing litter and stones) and placed into a numbered sealed bag for subsequent determination.

2.3 Laboratory analyses

The physiological traits of leaves were determined; the relative chlorophyll content of leaves was determined by a portable chlorophyll meter (CCM-200, Lanende, Shandong, China). The leaf structural traits were determined as follows: the leaf area (mm^2) was measured using a scanner (LIDE300, Canon, Guangdong, China), and the leaf thickness (mm) was measured using a vernier caliper (accurate to 0.01 mm). The saturated fresh weight (g) and dry weight (g) of the leaves were measured by an electronic balance. The specific leaf area was calculated as: specific leaf area (mm^2/g)=leaf area (mm^2)/leaf dry weight (g). The leaf dry matter content was calculated as: leaf dry matter content=leaf dry weight (g)/leaf saturated fresh weight (g). The plant leaf samples were dried and crushed at 65°C, and the soil samples were dried and ground naturally and sieved through 100 mesh. We determined the element content of the soil and plants according to Dong (1997). The contents of N, P, potassium (K), calcium (Ca), magnesium (Mg), and Ferrum (Fe) in

the soil and plants were determined by atomic absorption spectrometry. According to the study results conducted by Bao (2000) and Zheng (2013), we determined soil physical-chemical properties. Soil water content, pH, and soil electrical conductivity were measured by the drying method, potentiometric method, and electrical conductivity method, respectively.

The calculation formula of nutrient resorption is as follows:

$$\text{NuRE} = \frac{(\text{Nugreen} - \text{Nusenesced} \times \text{MLCF})}{\text{Nugreen}} \times 100\%\,, \tag{1}$$

where NuRE is the nutrient resorption efficiency (%); Nugreen is the nutrient concentration in the mature leaves (mg/g); Nusenesced is the nutrient concentration in the senescent leaves (mg/g); and MLCF is a mass loss correction factor used to compensate for leaf mass loss during senescence, where MLCF is based on the global average of 0.784 for deciduous plants (Vergutz et al., 2012).

2.4 Statistical analyses

SPSS 23.0, Origin 2018, and R 3.4.0 software were used for data processing and statistical analysis. One-way analysis of variance (one-way ANOVA) was used to compare the differences in resorption efficiency of different nutrient elements, leaf functional traits, and soil physical-chemical properties in different habitats and different plant leaves. The differences in resorption efficiency, leaf functional traits, and soil physical-chemical properties of the same plant in different habitats were tested by independent *t* test. Redundancy analysis (RDA) and Pearson correlation analysis were used to analyze the correlation between nutrient resorption efficiency and influencing factors of desert plant leaves.

In this study, the resorption efficiency of different elements of each plant was taken as the dependent variable, and the soil physical-chemical properties and leaf functional traits were taken as the explanatory variables. RDA screening and analysis were carried out after the standardization of these impact factors. The test results showed that they all had certain model contributions (the expansion coefficients of soil physical-chemical properties were all less than 20) and could be analyzed as environmental factor variables. At the same time, a Monte Carlo test was used to quantitatively evaluate the independent interpretation of each influencing factor on the resorption characteristics of each element.

3 Results

3.1 Leaf nutrient content characteristics of typical desert plants

The leaf nutrient content characteristics of the typical desert plants on the northern margin of the Tarim Basin are shown in Figure 1. The leaf N content (LNC), leaf P content (LPC), and leaf K content (LKC) in the mature leaves were higher than those in the senescent leaves, while the leaf Ca content (LCaC), leaf Mg content (LMgC), and leaf Fe content (LFeC) in the mature leaves were mostly lower than those in the senescent leaves. The LNC of *A. camelorum* was significantly higher than that of the other plants ($P<0.05$) in the mature and senescent leaves in both habitats. Except for *P. euphratica*, the LNC of the other plants was generally higher in Habitat I than in Habitat II. The LPC of *T. ramosissima* was lower than that of the other plants, and the LPC of most plants in Habitat I was significantly lower than that in Habitat II ($P<0.05$). The LKC of *A. camelorum* was significantly higher than that of the other three plants ($P<0.05$). In the two habitats, LKC was generally higher in Habitat I; the difference in LCaC among different plants was small, and the LCaC of most plants in Habitat I was lower than that of most plants in Habitat II ($P<0.05$); only *P. euphratica* showed the opposite trend. The LMgC of the plants was similar to the LCaC, mostly lower in Habitat I than in Habitat II ($P<0.05$), and the mature leaves of *G. inflata* and *A. camelorum* showed the opposite trend. The LFeC of *G. inflata* was significantly higher than that of the other plants ($P<0.05$). The LFeC of *T. ramosissima* and *A. camelorum* showed the opposite trend to that of other plants, as it was significantly lower in Habitat I than in Habitat II ($P<0.05$).

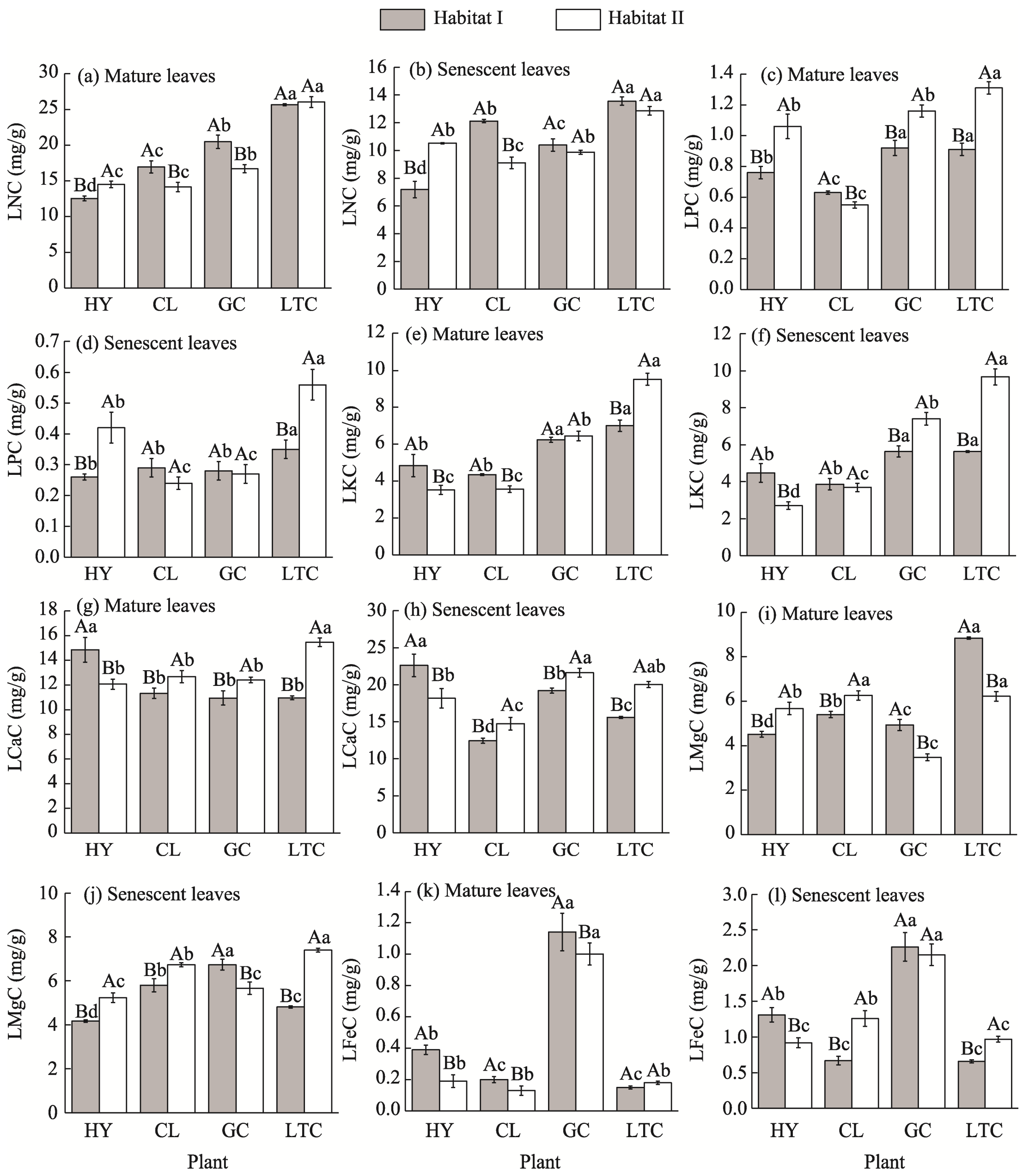

Fig. 1 Nutrient content characteristics of mature and senescent leaves of different plants in different habitats. (a and b), leaf nitrogen (N) content (LNC); (c and d), leaf phosphorus (P) content (LPC); (e and f), leaf potassium (K) content (LKC); (g and h), leaf calcium (Ca) content (LCaC); (i and j), leaf magnesium (Mg) content (LMgC); (k and l), leaf ferrum (Fe) content (LFeC). HY, *Populus euphratica* Oliv.; CL, *Tamarix ramosissima* Ledeb.; GC, *Glycyrrhiza inflata* Batal.; LTC, *Alhagi camelorum* Fisch.. Habitat I and Habitat II denote saline-alkali land and sandy land, respectively. Different lowercase letters represent significant differences among different plants in the same habitat (P<0.05), and different uppercase letters represent significant differences between different habitats for the same plant (P<0.05). Bars mean standard errors.

3.2 Characteristics of leaf nutrient resorption of typical desert plants

N, P, and K were resorbed in the leaves of the four plants; Ca was enriched in the leaves of *P. euphratica*, *G. inflate*, and *A. camelorum*; Mg was enriched in the leaves of *G. inflata*; and Fe was accumulated in the leaves of the four plants (Fig. 2). There was little difference in the NRE and PRE among the different plant leaves. The NRE of *P. euphratica* and *G. inflata* leaves in Habitat I

was significantly higher than that in Habitat II ($P<0.05$). The K resorption efficiency (KRE) of *P. euphratica* leaves was higher than that of the other plants. The KRE of most plant leaves was significantly higher in Habitat I than in Habitat II ($P<0.05$). Except for *T. ramosissima*, the Ca resorption efficiency (CaRE) of most plant leaves was negative, and the Ca enrichment degree of *A. camelorum* was significantly higher in Habitat I than in Habitat II ($P<0.05$). The Mg resorption efficiency (MgRE) of the *G. inflata* leaves was negative, and the other three plant leaves resorbed Mg. Except for *T. ramosissima*, there was no significant difference in Fe resorption efficiency (FeRE) among the four plants between the two habitats.

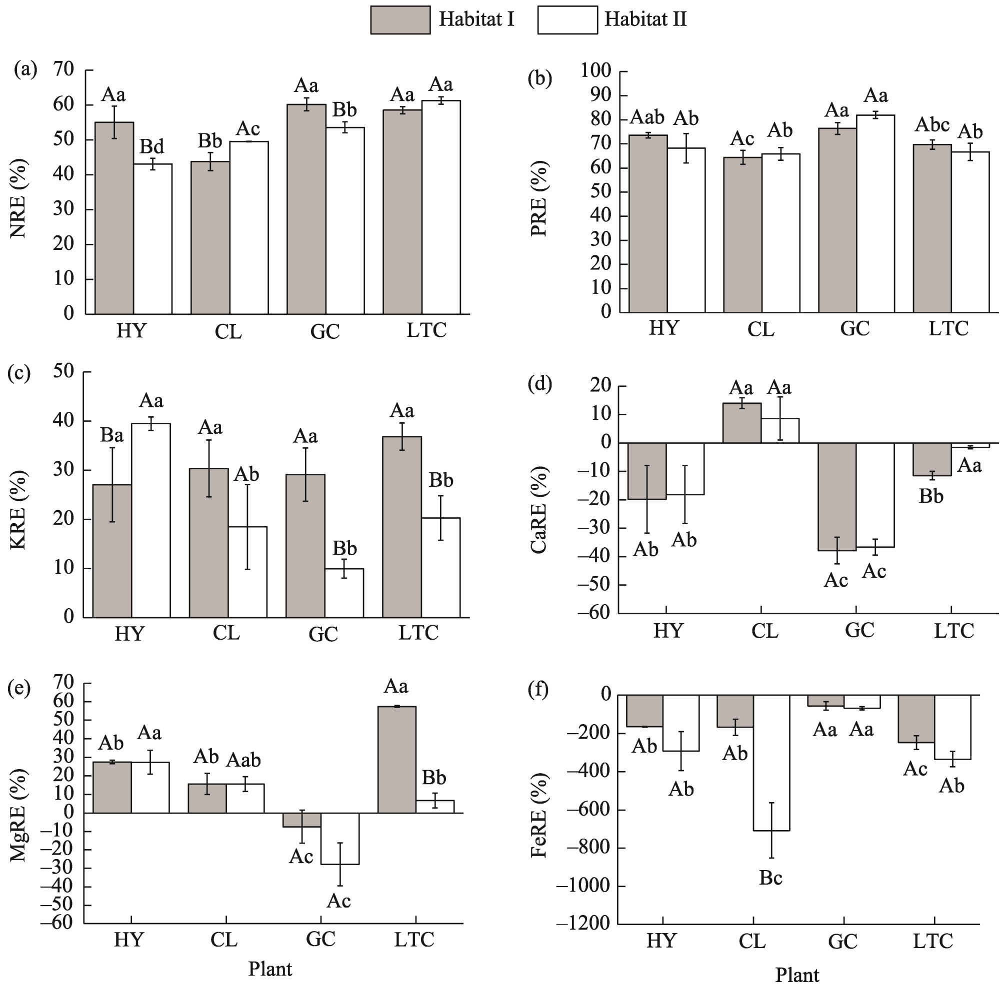

Fig. 2 Nutrient resorption efficiency of different plant leaves in different habitats. (a), N resorption efficiency (NRE); (b), P resorption efficiency (PRE); (c), K resorption efficiency (KRE); (d), Ca resorption efficiency (CaRE); (e), Mg resorption efficiency (MgRE); (f), Fe resorption efficiency (FeRE). Different lowercase letters represent significant differences among different plants in the same habitat ($P<0.05$); and different uppercase letters represent significant differences between different habitats for the same plant ($P<0.05$). Bars mean standard errors.

3.3 Leaf functional traits and soil physical-chemical properties of typical desert plants

The leaf functional traits of the typical desert plants are shown in Figure 3. The leaf thickness of *T. ramosissima* was significantly higher than that of the other plants ($P<0.05$), and there was no significant difference in leaf thickness between the two habitats. The leaf dry matter content of *A. camelorum* was lower than that of other plants. The leaf dry matter content of *T. ramosissima* and *G. inflata* in Habitat II was significantly higher than that in Habitat I ($P<0.05$). The specific leaf

area of *P. euphratica* was significantly higher than that of the other species ($P<0.05$), and there was no significant difference in the specific leaf area of each plant in the different habitats. The relative chlorophyll content of *T. ramosissima* was significantly lower than that of the other species ($P<0.05$), and the relative chlorophyll content of most plants in Habitat I was significantly higher than that of most plants in Habitat II ($P<0.05$).

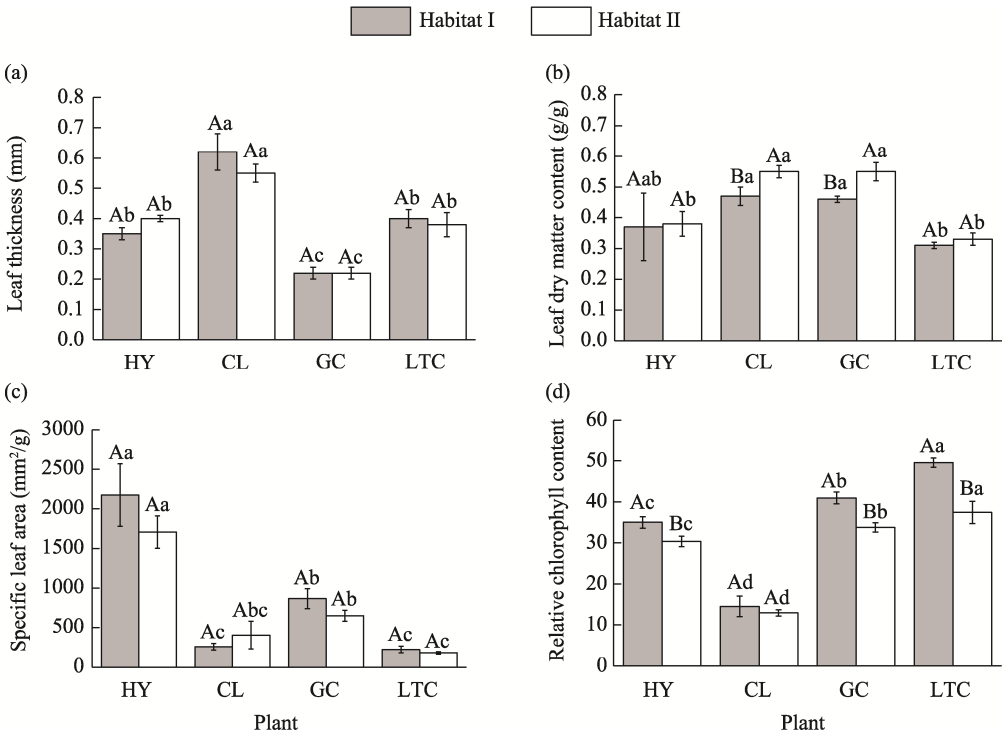

Fig. 3 Functional traits of plant leaves in different habitats. (a), leaf thickness; (b), leaf dry matter content; (c), specific leaf area; (d), relative chlorophyll content. Different lowercase letters represent significant differences among different plants in the same habitat ($P<0.05$), and different uppercase letters represent significant difference between different habitats for the same plant ($P<0.05$). Bars mean standard errors.

As shown in Table 1, the soil water content in the study area was low, ranging from 1.62% to 4.49%, and the soil water content under the plant canopy of Habitat I was higher than that of Habitat II. The soil was alkaline, and the highest value of soil pH was 9.78. The soil pH value of *P. euphratica* was significantly higher than that of other plants. The soil electrical conductivity of each plant in Habitat I was generally higher than that of each plant in Habitat II; the soil nutrient content was generally low, and the soil N content under the canopy of *P. euphratica* was relatively high. The soil N content under the canopy of each plant was generally higher in Habitat I than in Habitat II. The contents of P, K, Ca, Mg, and Fe in the soil under the plant canopy were not significantly different.

3.4 Effects of soil physical-chemical properties and leaf functional traits on nutrient resorption efficiency

RDA showed that leaf functional traits and soil physical-chemical properties explained 78.6% and 1.4% of the variance in RDA1 and RDA2, respectively (Fig. 4). The first two ordination axes explained 80.0% of the relationship of leaf functional traits and soil physical-chemical properties with nutrient resorption efficiency. According to the RDA results in Figure 4a, soil Ca content, soil Fe content, specific leaf area, and relative chlorophyll content were positively correlated with the NRE, PRE, and FeRE. Soil P content, soil K content, and leaf thickness were negatively correlated with the resorption efficiency of these three elements. Soil K content, soil electrical

Table 1 Soil physical-chemical properties under plant canopy in different habitats

Soil physical-chemical property	Habitat I				Habitat II			
	HY	CL	GC	LTC	HY	CL	GC	LTC
SWC (%)	4.49±2.61^{Aa}	4.53±2.51^{Aa}	3.03±0.72^{Aa}	2.97±0.34^{Aa}	1.94±0.17^{Aa}	2.18±1.11^{Aa}	1.65±0.81^{Aa}	1.62±1.33^{Aa}
Soil pH	9.78±0.24^{Aa}	8.27±0.03^{Ab}	8.05±0.07^{Ab}	8.11±0.13^{Ab}	8.72±0.30^{Ba}	8.06±0.13^{Ab}	8.04±0.15^{Ab}	8.19±0.05^{Ab}
EC (mS/cm)	3.70±0.36^{Aa}	4.03±0.23^{Aa}	1.70±0.10^{Ab}	1.83±0.75^{Ab}	1.33±0.31^{Ba}	1.90±0.75^{Ba}	1.33±0.50^{Aa}	0.83±0.42^{Aa}
Soil N (mg/g)	0.23±0.02^{Aa}	0.17±0.02^{Ab}	0.10±0.01^{Ac}	0.08±0.01^{Ac}	0.09±0.02^{Ba}	0.08±0.01^{Bab}	0.06±0.01^{Bc}	0.06±0.01^{Bc}
Soil P (mg/g)	0.68±0.00^{Bc}	0.77±0.03^{Aa}	0.71±0.03^{Ab}	0.71±0.04^{Aab}	0.81±0.02^{Aa}	0.82±0.18^{Aa}	0.83±0.08^{Aa}	0.80±0.03^{Aa}
Soil K (mg/g)	17.01±0.48^{Aa}	16.67±0.24^{Aa}	17.03±0.16^{Aa}	17.18±0.09^{Aa}	16.61±0.35^{Aab}	17.20±0.29^{Aa}	16.05±0.67^{Ab}	15.71±0.50^{Bb}
Soil Ca (mg/g)	52.66±3.09^{Aa}	53.77±6.24^{Aa}	52.49±2.32^{Aa}	46.72±3.18^{Aa}	51.34±2.71^{Aa}	52.18±4.03^{Aa}	55.89±4.84^{Aa}	52.65±1.91^{Aa}
Soil Mg (mg/g)	11.44±0.35^{Aa}	11.30±0.63^{Aa}	10.16±0.14^{Ab}	10.07±0.30^{Ab}	10.31±0.44^{Ba}	10.41±0.37^{Aa}	10.32±1.41^{Aa}	10.34±0.17^{Aa}
Soil Fe (mg/g)	24.83±2.18^{Aa}	24.10±1.03^{Aa}	23.56±0.82^{Aa}	24.41±0.30^{Aa}	22.88±0.14^{Aa}	23.18±0.51^{Aa}	25.35±2.29^{Aa}	25.21±1.33^{Aa}

Note: SWC, soil water content; EC, soil electrical conductivity; soil N, soil nitrogen content; soil P, soil phosphorus content; soil K, soil potassium content; soil Ca, soil calcium content; soil Mg, soil magnesium content; soil Fe, soil ferrum content. HY, *Populus euphratica* Oliv.; CL, *Tamarix ramosissima* Ledeb.; GC, *Glycyrrhiza inflata* Batal.; LTC, *Alhagi camelorum* Fisch.. Habitat I and Habitat II denote saline-alkali land and sandy land, respectively. Different lowercase letters represent significant differences among different plants in the same habitat (P<0.05), and different uppercase letters represent significant difference between different habitats for the same plant (P<0.05). Mean±SE.

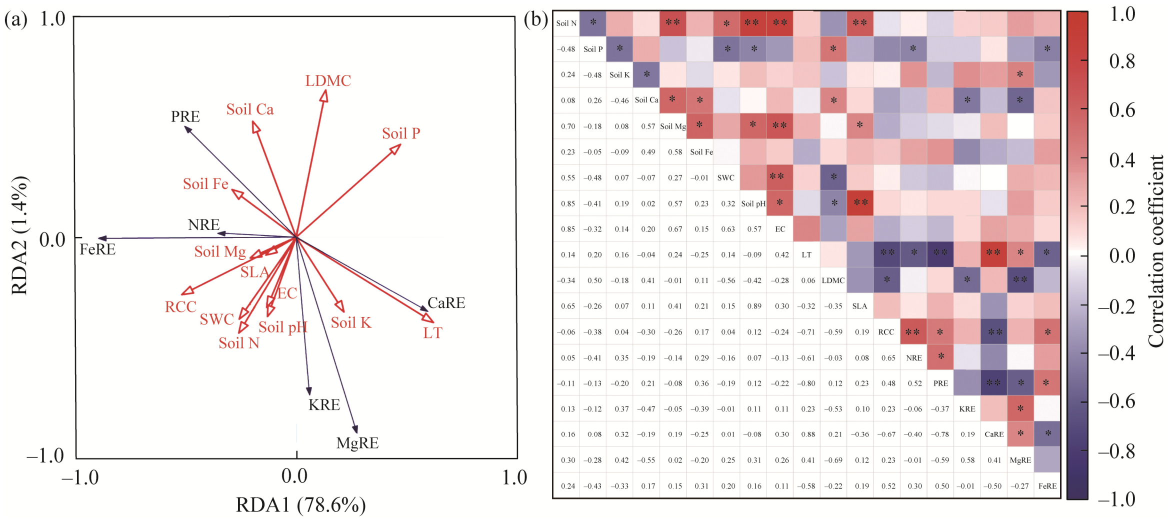

Fig. 4 Redundancy analysis (RDA; a) and correlation heat map (b) of soil physical-chemical properties, leaf functional traits, and nutrient resorption efficiency. soil N, soil nitrogen content; soil P, soil phosphorus content; soil K, soil potassium content; soil Ca, soil calcium content; soil Mg, soil magnesium content; soil Fe, soil ferrum content. SWC, soil water content; EC, soil electrical conductivity; LT, leaf thickness; LDMC, leaf dry matter content; SLA, specific leaf area; RCC, relative chlorophyll content. **, P<0.01 level; *, P<0.05 level.

conductivity, soil pH, and leaf thickness were positively correlated with the KRE, MgRE, and CaRE. Soil P content, soil Ca content, soil Fe content, and leaf dry matter content were negatively correlated with the resorption efficiency of these three elements.

The correlation matrix among leaf functional traits, soil physical-chemical properties, and nutrient resorption efficiency is shown in Figure 4b. The results showed that the NRE had a strong correlation with relative chlorophyll content and leaf thickness, and the correlation coefficients were 0.65 and –0.61, respectively. The PRE had a strong correlation with leaf thickness, and the correlation coefficient was –0.80. The KRE had a strong correlation with soil Ca content and leaf dry matter content, and the correlation coefficients were –0.47 and –0.53, respectively. The CaRE had a strong correlation with leaf thickness and relative chlorophyll content, and the correlation coefficients were 0.88 and –0.67, respectively. The MgRE had a

strong correlation with leaf thickness, soil Ca content, and leaf dry matter content, and the correlation coefficients were 0.41, –0.55, and –0.69, respectively. The FeRE had a strong correlation with relative chlorophyll content, soil P content, and leaf thickness, and the correlation coefficients were 0.52, –0.43, and –0.58, respectively.

Based on the above research, we carried out a Monte Carlo test on these 13 influencing factors, and the importance ranking of these influencing factors was obtained. The results are shown in Table 2. The order of importance of the influencing factors on the nutrient resorption efficiency of plants was as follows: leaf thickness, soil electrical conductivity, soil P content, soil K content, soil pH, soil N content, relative chlorophyll content, specific leaf area, leaf dry matter content, soil Mg content, soil Ca content, soil Fe content, and soil water content. Among these factors, leaf thickness had an extremely significant effect on the nutrient resorption efficiency of plants ($P<0.01$), and soil electrical conductivity and soil P content had a significant effect on the nutrient resorption efficiency of plants ($P<0.05$). The proportions of leaf thickness, soil electrical conductivity, and soil P content to all influencing factors were 30.7%, 17.5%, and 10.4%, respectively, indicating that these three factors were the main factors affecting the nutrient resorption efficiency of plants.

Table 2 Results of the Monte Carlo test for soil physical-chemical properties and leaf functional traits

Influencing factor	Explanation (%)	*F* value	*P* value
Leaf thickness	30.7	9.7	0.010
Soil electrical conductivity	17.5	7.1	0.012
Soil P	10.4	5.7	0.034
Soil K	6.9	3.1	0.102
Soil pH	3.4	2.0	0.186
Soil N	2.8	1.7	0.202
Relative chlorophyll content	1.3	0.8	0.370
Specific leaf area	2.0	1.2	0.270
Leaf dry matter content	1.8	1.1	0.314
Soil Mg	0.8	0.5	0.466
Soil Ca	2.3	1.4	0.256
Soil Fe	0.6	0.4	0.594
Soil water content	0.1	<0.1	0.850

4 Discussion

4.1 Nutrient resorption characteristics of typical desert plant leaves in different habitats

The nutrient resorption characteristics of plant leaves reflect not only the adaptation mechanism of plants to the environment but also one of the key strategies for plants to use nutrients efficiently. There are some differences in soil nutrient supply capacity in the two habitats, so the nutrient resorption efficiency of each plant in the two habitats also shows different degrees.

N, P, and K are the main elements limiting plant growth and are involved in various important physiological regulation processes in plants. The results of this study showed that the NRE and KRE of most plants in both habitats were lower than the global mean of terrestrial plants (62.1% and 70.1%, respectively), while the PRE was higher than the global mean of terrestrial plants (64.9%; Vergutz et al., 2012). The lower NRE and KRE may have been related to factors such as species and growth environment. The high PRE of each plant in this study indicated that the growth of these plants may have been limited by P. At the same time, plant nutrient resorption efficiency in different habitats will also show some differences. Liu et al. (2015) have shown that

the nutrient supply capacity of a system is a major factor limiting plant growth and that plants growing in habitats with low nutrient supply capacity have lower nutrient resorption rate. The resorption efficiency of N, P, and K in most desert plants was higher in Habitat I than in Habitat II, which was related to the higher soil nutrient content and higher nutrient supply capacity in Habitat I than in Habitat II. Ca plays an important role in maintaining the physiological balance and stability of plant leaf cells. Zhou et al. (2016) found that plants can reduce the toxicity of Na in vivo by regulating the absorption of Ca, thereby alleviating the damage to cell membranes due to environmental stress. The CaRE in the leaves of *P. euphratica*, *G. inflate*, and *A. camelorum* was negative under the harsh conditions of water shortages, high temperatures, and high salinity levels on the northern margin of the Tarim Basin, indicating that Ca accumulated in the senescent leaves of these plants. In this study, the soil salinization of Habitat I was higher than that of Habitat II, and the CaRE of *A. camelorum* enrichment degree in Habitat I is higher than that in Habitat II. *A. camelorum* may adapt to high-salt habitats by enriching more Ca. Mg is an important component of chlorophyll, and its content in leaves is related to the strength of leaf photosynthetic function (Zhang, 2018). In this study, only the MgRE of *G. inflata* was negative, which may have been related to the biological characteristics of *G. inflata* itself. The growth rate of *G. inflata* is fast, and its leaves need to use more Mg to synthesize more chlorophyll to enhance photosynthetic capacity; thus, it continues to accumulate in senescent leaves. As a trace element, Fe also plays an important role in plant growth but has received relatively little attention. The four plants in the two habitats on the northern margin of the Tarim Basin had negative FeRE values, which may have been due to the high Fe content in the mature leaves. Plants can meet their growth needs through root absorption without activating nutrients from old leaves, which is consistent with the conclusions of Zhou et al. (2022).

4.2 Leaf functional traits of typical desert plants and physical-chemical properties of soil under canopy in different habitats

Leaf thickness and leaf dry matter content can characterize the self-protection mechanism and nutrient retention ability of plants (Zhang et al., 2016). This study found that *T. ramosissima* had greater leaf thickness and leaf dry matter content than those of the other plants in both habitats. The leaves of *T. ramosissima* are green assimilating branches, and their unique leaf morphology makes them better able to reduce evaporation to adapt to arid habitats. At the same time, the accumulation of leaf dry matter content in several plants in Habitat II was relatively high, which also reflected the adaptive change strategy of plants to drought-related leaf functional traits (Pescador et al., 2015). The specific leaf area and relative chlorophyll content of plants are related to the utilization efficiency of resources and the ability of plants to obtain light resources (Wang et al., 2022). The specific leaf area of *P. euphratica* was significantly higher than that of the other plants, and it is the dominant tree on the northern margin of the Tarim Basin. The high specific leaf area reflects the efficient resource utilization strategy of *P. euphratica*, and the advantage of plant height can also allow it to obtain more light resources to obtain more living space and adapt to habitats with limited resources. The relative chlorophyll contents of *G. inflata* and *A. camelorum* were higher than those of the other plants. As herbs, these two plants increase their growth rate through a more efficient photosynthetic rate to utilize and obtain resources in the environment, and thus, they are the quick investment-return species proposed by Osnas et al. (2013). In addition, the relative chlorophyll contents of the plants in Habitat I were higher than those of the plants in habitat II, which may have been related to the different soil water contents and nutrient supplies in the two habitats. Studies have shown that soil water content and soil mineral element content affect the relative chlorophyll content in plants. Low water content will indirectly inhibit the synthesis of chlorophyll in plants, and N deficiency will hinder chlorophyll synthesis (Wang et al., 2022), which is consistent with the results of this study.

The northern margin of the Tarim Basin is located in an extremely arid area, with severe habitat water shortages and soil desertification and salinization. Therefore, the soil water content under the plant canopy in this study was generally below 5.00%, soil was alkaline, and soil electrical

conductivity was relatively high. The soil in the study area was relatively barren, and the contents of soil N (0.11 mg/g), K (16.70 mg/g), and Fe (24.20 mg/g) were lower than the national average level measured by Chen et al. (1991) as N (0.84 mg/g), K (18.00 mg/g), and Fe (28.00 mg/g). Finally, the soil moisture and nutrient content of Habitat I were higher than those of Habitat II, and the soil nutrient supply affects the resorption efficiency of plant leaves.

4.3 Relationship of nutrient resorption efficiency with leaf functional traits and soil physical-chemical properties

The resorption of element nutrients is related to the specific species and environmental factors. Leaf thickness, soil electrical conductivity, and soil P content were the main factors affecting the nutrient resorption of the desert plants growing in the desert area of northern margin of the Tarim Basin.

Leaves with high leaf thickness can help plants better resist physical damage. The results of this study showed that leaf thickness was negatively correlated with NRE, PRE, and FeRE, which was different from the results of previous studies (Liu et al., 2015; Zhou et al., 2022). The effect of leaf thickness may be related to leaf life. Long-lived leaves usually have higher nutrient use efficiency than short-lived leaves. To adapt to harsh environments such as drought and pests, desert plants with high leaf thickness may use more nutrients to construct defensive tissues for self-protection, which may not be conducive to the resorption, transfer, and reuse of plants. However, how plants adapt to environmental changes through the trade-off strategy between leaf functional traits and nutrient resorption is still unclear, and the internal mechanism remains to be further explored.

In this study, soil electrical conductivity was positively correlated with the resorption efficiency of most elements. The higher the degree of soil salinization in the study area, the stronger the soil salinity, usually the lower the availability of soil nutrients, and plants were less likely to obtain nutrients from the soil. Plants need to transfer more elements from senescent leaves to meet the needs of growth, thereby resisting the stressful saline-alkali habitat, so the resorption efficiency is higher. Study conducted by Flowers et al. (2008) also confirmed that many halophytes in saline-alkali habitats have higher protein contents, and the saline-alkali environment has a stimulating effect on the growth of these plants, resulting in them usually having higher nutrient resorption capacity. In nutrient-limited soil and high-salinity soil, soil moisture and nutrients are easily lost and difficult to replenish. The supply of soil nutrients in such habitats will become the main factor limiting plant growth. The P content of desert soil on the northern margin of the Tarim Basin is negatively correlated with the resorption efficiency of most elements in plant leaves. The PRE of each plant was higher than the resorption efficiency of the other elements, indicating that the growth of these plants was limited by P. Studies have shown that when the nutrient imbalance of plant habitats limits the growth of plants by a certain element, plants will have higher resorption efficiency for this limiting element (Li et al., 2021). At the same time, the ability of plant nutrient resorption was lower in soils with higher P content, which was consistent with the current study results. With the increase of soil nutrient contents, the efficiency of plant leaf nutrient resorption decreases (Aerts, 1996; Kobe et al., 2005), which is also an adaptive nutrient regulation mechanism of plants to the environment.

5 Conclusions

P. euphratica, *T. ramosissima*, *G. inflate*, and *A. camelorum* are typical dominant desert plants growing in the desert area of the northern margin of the Tarim Basin. Their adaptation strategies to desert habitats can provide a theoretical basis for screening viable plants in the region. Through the study of nutrient resorption and its influencing factors, it was found that the four plants reabsorbed N, P, and K, which further confirmed the strategy of desert plants to adapt to barren habitats through nutrient resorption efficiency. Ca was enriched in the leaves of *P. euphratica*, *G. inflate*, and *A. camelorum*, and the enrichment degree increased with increasing soil salinization

degree, reflecting that plants adapted to habitats with different degrees of salinization by adjusting the nutrient resorption efficiency of Ca. The leaves of *G. inflata* were enriched in Mg, and Fe was enriched in the leaves of the four plants. *T. ramosissima* had greater leaf thickness and leaf dry matter content, *P. euphratica* had higher specific leaf area, and *G. inflata* and *A. camelorum* had higher relative chlorophyll contents. Leaf thickness, soil electrical conductivity, and soil P content were the main factors affecting the nutrient resorption efficiency of these four plants. In the arid, saline-alkali, and barren habitats on the northern margin of the Tarim Basin, different plants have evolved different survival strategies. The coordinated evolution between leaf functional traits and nutrient resorption efficiency of different plants is the embodiment of adaptability to special habitats, but the internal mechanism of the trade-off between them needs to be further studied.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Conceptualization: GONG Lu; Data curation: ZHOU Chongpeng; Methodology: ZHOU Chongpeng; Investigation: ZHOU Chongpeng; Formal analysis: ZHOU Chongpeng; Writing - original draft preparation: ZHOU Chongpeng; Writing - review and editing: GONG Lu, WU Xue, LUO Yan; Funding acquisition: WU Xue; Resources: GONG Lu, WU Xue; Supervision: GONG Lu; Project administration: WU Xue; Software: ZHOU Chongpeng; Validation: GONG Lu; Visualization: ZHOU Chongpeng.

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